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## SUITABILITY OF OYSTER RESTORATION SITES ALONG THE LOUISIANA COAST: EXAMINING SITE AND STOCK × SITE INTERACTION

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**ABSTRACT** Recognition of the global loss of subtidal oyster reefs has led to a rise in reef restoration efforts, including in the Gulf of Mexico. Created reef success depends entirely on selecting a location that supports long-term oyster growth and survival, including the recruitment and survival of on-reef oysters. Significant changes in estuarine salinity through management of freshwater inflows and through changed precipitation patterns may significantly impact the locations of optimal oyster restoration sites. These rapid shifts in conditions necessitate a need to better understand both impacts to on-reef oyster growth and population development, and variation in oyster stock performance. Oyster growth, mortality, condition, and disease prevalence were examined in three different stocks of oysters located in protected cages, as well as oyster recruitment and mortality on experimental reef units in three different locations representing a salinity gradient, along the Louisiana Gulf coast in 2011 and 2012. Over a 2-y period, the high-salinity site had highest oyster growth rate in protected cages but demonstrated the least likelihood for reef development based on on-reef oyster population failure, likely because of predation-related mortality (high recruitment and 100% mortality). In contrast, the mid-salinity site with moderate oyster growth and on-reef recruitment and low mortality demonstrated a higher likelihood for reef development. The lowest salinity site exhibited extreme variability in all oyster responses between years because of extreme variation in environmental conditions during the study, indicating a low likelihood of long-term reef development. Whereas limited differences in stock performance between sites were found, the range of site environmental conditions tested was ultimately much lower than expected and may not have provided a wide enough range of conditions. In areas with limited, low recruitment, or rapidly changing environmental conditions, seeding with stocks selected for best growth and survival under expected future environmental conditions could better ensure reef development by using oyster populations best suited to the predicted conditions. With rapidly changing estuarine conditions from anthropogenic activities and climate change, siting of oyster reef restoration incorporating both oyster population dynamics and *in situ* biotic and abiotic interactions is critical in better directing site selection for reef restoration efforts.

**KEY WORDS:** eastern oyster, *Crassostrea virginica*, Gulf of Mexico, estuaries, oyster stock, salinity, subtidal reef, location

### INTRODUCTION

Restoring foundation species to build lost or degraded habitat inherently requires understanding biotic and abiotic drivers of the foundation species. A key foundation species in coastal waters, oysters are dependent on recruitment, growth, and survival to build their reefs. In the Gulf of Mexico (GoM), where subtidal oyster reefs are impacted by harvest, anthropogenic changes in local hydrology, tropical cyclones, and degraded water quality, reef loss is estimated to be between 50% and 89% (Beck et al. 2011). Recognition of this loss, and the subsequent loss of associated ecological services, has led to a diversity of reef restoration and creation projects in the GoM (Scyphers et al. 2011, La Peyre et al. 2014). Whereas created oyster reefs may vary widely in design to suit local bathymetry and material availability, they are all dependent on ultimately developing a healthy, self-sustaining oyster population (Soniati et al. 2004).

The distribution of natural eastern oyster (*Crassostrea virginica*) reefs depends on a combination of physical and biological factors that greatly influence specific stages within the oyster's life cycle (Livingston et al. 2000). Of all the abiotic factors that affect oyster health, temperature and salinity play the largest role in oyster success (Shumway 1996). Alone and synergistically, these two factors control virtually every aspect of oyster feeding, respiration, gonadal development, time and

rate of spawning, growth, and mortality. Although tolerant to a wide range of temperature (−2–36°C, Shumway 1996) and salinity (0–42.5, Shumway 1996), the frequency, timing, length of exposure, and interaction of temperature and salinity influence reproductive timing and success, oyster survival, and growth rates and are used in virtually all oyster models and suitability indices (e.g., Cake 1983, Soniat & Brody 1988, Barnes et al. 2007, Beseres Pollack et al. 2012). Restoration of sustainable oyster reef in the GoM requires identifying the range and characteristic environmental conditions (i.e., salinity and temperature) which support not just good oyster reproduction and growth but also survival or refuge from predation, competition (Soniati et al. 2004, Melancon et al. 2013), and disease (La Peyre et al. 2003).

A number of models have been developed as predictors of oyster habitat quality (Soniati & Brody 1988, Barnes et al. 2007, Beseres Pollack et al. 2012, Soniat et al. 2012). These different models rely predominantly on identifying areas with suitable spawning period salinities and examining annual mean and minimum salinity. These models help refine location selection; however, a better understanding of how salinity and temperature influence biological interactions such as predation, competition, or disease can ultimately assist in the development of a sustainable oyster population (Abbe & Breitburg 1992, Melancon et al. 2013, La Peyre et al. 2017). For example, oyster drills and mud crabs may decimate newly settled oysters (Butler 1985), whereas mussels may compete for space (Melancon et al. 2013, La Peyre et al. 2017), and under the right conditions,

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disease may negatively impact oyster populations (La Peyre et al. 2003, Powell 2017). Failure to incorporate on-reef biotic interactions may result in overly optimistic site selections.

In addition, there is growing evidence that local adaptation may affect oyster population responses to salinity and temperature combinations (Barber et al. 1991, Dittman et al. 1998, Brown et al. 2005, Burford et al. 2014) and should be considered in restoration activities (Leonhardt et al. 2017, Eierman & Hare 2016). Specifically, Leonhardt et al. (2017) compared growth and mortality of several Louisiana oyster stocks in variable salinity regimes, finding that stocks performed differently at different locations. Eierman and Hare (2016) demonstrated extensive genetics  $\times$  environment effects for low- and high-salinity oyster populations, suggesting a need to consider potential source populations for natural recruitment or seeding of restoration sites. This work is relevant for restoration in areas with rapidly changing environmental conditions or in areas lacking a source population. For example, where local recruitment may be low or nonexistent or where environmental conditions are rapidly changing because of human intervention, identifying oyster stocks that may enhance the local population may provide another potential tool to enhance oyster survival on newly created substrates (Wallace et al. 2002, Rodney & Paynter 2006, Grizzle et al. 2006, Brumbaugh & Coen 2009, Geraldi et al. 2013). More explicit suitability models may be beneficial in determining where to seed reefs with live oysters, as well as where to plan cultch.

Although estuarine systems are by definition highly variable, recent anthropogenic management activities combined with climate change may be changing the environmental conditions and characteristics more rapidly than in the past. Specifically, significant changes in estuarine salinity through management of freshwater inflows and through changed precipitation patterns affect salinity means and extremes, which may significantly impact the locations of optimal oyster-growing areas (Klinck et al. 2002, Wang et al. 2017). Furthermore, recent analyses suggest a decline in population reproductive capacity (Powell 2017). These rapid shifts necessitate a need to better understand both impacts to on-reef oyster growth and population development and variation in oyster stock performance.

This study examined oyster growth and mortality in different stocks of oysters located in predator-free cages, as well as recruitment and mortality on experimental reefs at three sites representing different salinity regimes across coastal Louisiana. Specifically, at each site, this study examined (1) oyster growth, mortality, and disease prevalence in predator-free cages to compare the effects of water quality, (2) on-reef oyster recruitment and survival to compare the effects of water quality and predation, and (3) oyster growth, mortality, and disease prevalence of three oyster stocks in predator-free cages to compare the effects of water quality between stocks. Ultimately, the success of created reefs requires locations that support oyster recruitment, survival, and growth; as recruitment becomes a limiting factor at restoration sites, identifying stock  $\times$  environment interactions becomes increasingly important.

## MATERIALS AND METHODS

### Study Sites

This study was conducted at three different estuarine locations along the Louisiana Gulf of Mexico coast: Vermilion

Bay [VB (29° 36' 39.99"N, 92° 3'19.70"W)], Sister (Caillou) Lake [SL (29° 12' 50.70"N, 90° 56' 3.12"W)], and Grand Isle [GI (29° 13'48.22"N, 90° 0'56.96"W)]. These sites were chosen as they cover a wide range of environmental conditions and represent areas where recent oyster restoration efforts have occurred (i.e., La Peyre et al. 2013a, 2013b, 2017; Fig. 1). This region is microtidal ( $0.3 \text{ m} \pm 0.03$  National Geodetic Vertical Datum), and water levels are driven more by wind events.

Vermilion Bay is a shallow, relatively fresh bay located in south central Louisiana (mean 5-y salinity based on daily measurements, 2008–2013,  $4.5 \pm 0.1$ ; United States Geological Survey Continuous Data Recorder (USGS CDR): 7387040; <https://la.water.usgs.gov/hydrowatch.html>). The study area in VB is characterized by shallow mean water depths ( $<1 \text{ m}$ ) and located adjacent to one of Louisiana's historic public oyster seed grounds; however, increased freshwater input from the Atchafalaya River has greatly diminished oyster production in recent years (Louisiana Department of Wildlife and Fisheries 2010).

Sister Lake has been a designated Public Oyster Seed Reservation since 1940 (Louisiana Department of Wildlife and Fisheries 2010). Approximately 30% of the area consists of subtidal reefs. Continued cultch deposition has allowed for the sustained public harvesting of oysters. Sister Lake is primarily an open body of water 1–3 m in depth, surrounded by brackish marsh. The mean 5-y (2008–2013) salinity is  $11.8 \pm 0.1$  (USGS CDR: 7381349; <https://la.water.usgs.gov/hydrowatch.html>).

Grand Isle is a barrier island located in southeastern Louisiana. The island is at the mouth of Barataria Bay, where it meets the GoM. The Louisiana Sea Grant Research Hatchery is located on the bay side of this island. The mean 5-y salinity (2008–2013) is  $19.6 \pm 0.2$  (USGS CDR: 73802516; <https://la.water.usgs.gov/hydrowatch.html>).

### Water Quality

Salinity and temperature ( $^{\circ}\text{C}$ ) data for the period of study (January 2011 through December 2012) were obtained from USGS CDR within SL and GI and VB used water quality data from Louisiana's Coastwide Reference Monitoring System (CRMS0541; CPRA 2016) as this recorder was available and matched more closely discrete measures of salinity at this site. For all sites, daily means were downloaded. Interval salinity and temperature means were calculated as the mean salinity or temperature between each sampling period.

### Oysters

All seed oysters used for off-reef assessment of growth and mortality were obtained from the Louisiana Sea Grant Research Hatchery located at the Louisiana Department of Wildlife and Fisheries facility in Grand Isle, LA. Oysters used in 2011 were the progenies of a Breton Sound (BS) brood stock spawned in June 2010. They were maintained at the Sea Grant Hatchery in an adjustable longline system (ALS, BST Oyster Co., Cowell, South Australia) until their deployment at each study site in February 2011. Mean shell height (SH) at the time of deployment was  $68.8 \pm 0.6 \text{ mm}$ . Oysters used in 2012 were the progenies of three brood stocks originally collected from BS, SL, and Lake Calcasieu (LC), Louisiana. Each brood stock was

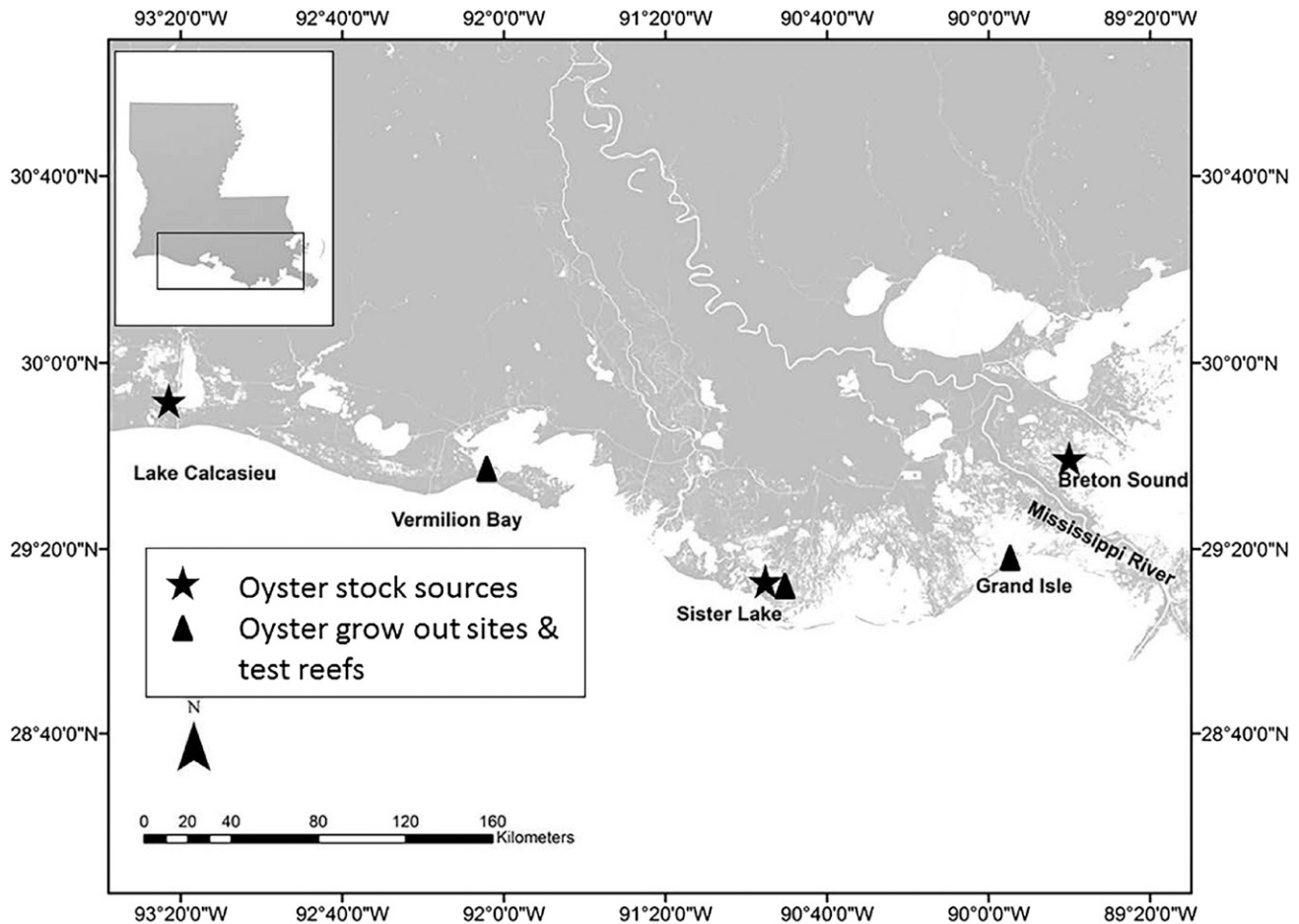


Figure 1. Map of Louisiana's Gulf of Mexico coast, including the three study areas: Vermilion Bay, Sister Lake, and Grand Isle, and locations of source stock oysters.

spawned in June 2011 at the hatchery, and their progenies were maintained separately in the Australian Longline System (ALS) in GI until deployment at each study site in December 2011. At the time of deployment, mean SH (mean SE) was similar for all oysters—BS ( $62.2 \pm 0.8$  mm), SL ( $63.5 \pm 0.8$  mm), and LC ( $60.4 \pm 0.7$  mm).

#### *Off-Reef Mortality, Growth, Condition, and Parasitic Infection—Site Comparison*

In February 2011, two ALS bags containing fifty (50) BS stock seed oysters each were placed at each site (2 bags  $\times$  3 sites  $\times$  50 oysters). Bags were attached to polyvinyl chloride poles and kept 10–20 cm off the water bottom to prevent burial. Bags were sampled every two months by measuring SH to the nearest 10th of a millimeter using a digital caliper and recording the number of dead oysters within each bag until October 2011. Interval growth rate [IGR =  $(SH_{t2} - SH_{t1})/mo$ ;  $mm\ mo^{-1}$ ] and mortality (%) were calculated as a mean per bag and reported for each sample period. Every 4 mo (February, June, and October), 15 oysters were haphazardly removed from each bag to evaluate condition index and infection intensity by the protistan parasite *Perkinsus marinus*, as described in Condition Index and Parasitic Infection.

#### *Off-Reef Mortality, Growth, Condition, and Parasitic Infection—Stock Comparison*

In December 2011, three ALS bags, each containing 50 oysters from one of the three oyster stocks, were deployed at each site (3 stocks  $\times$  3 sites  $\times$  50 oysters = 450 oysters) following the same set up described previously. To increase statistical power, small plastic identification tags (FT-LF-97; FLOYTAG Inc., Seattle, WA) were glued to each oyster to track individual growth rates. Interval growth rate ( $mm\ mo^{-1}$ ) is reported as a mean per oyster whereas mortality (%) reports mean bag mortality. Every four months (December, April and August), fifteen oysters were haphazardly removed from each bag to evaluate condition index and infection intensity by the protistan parasite *Perkinsus marinus*, as described in Condition Index and Parasitic Infection.

#### *Condition Index and Parasitic Infection*

Condition index was determined by calculating the ratio of dry tissue weight to dry shell weight (Lucas & Beninger 1985). For each oyster, a 10 ml aliquot of oyster tissue homogenate was prepared to determine *Perkinsus marinus* infection intensity. The tissue was dried at 60°C for 48 h, and the dry weight for the whole-oyster tissue was calculated based on the total volume



of homogenized tissue as described by La Peyre et al. (2003). Shells were cleaned of sediment and attached biofouling, dried at 60°C for 48 h, and weighed (g). The number of parasites per gram of oyster tissue was determined using the whole-oyster procedure as described by Fisher and Oliver (1996) and modified by La Peyre et al. (2003). Infection intensity is reported as the number of parasites per gram of oyster wet tissue.

#### Experimental Reef Unit Population Demography and Density

Substrate blocks used as experimental reef units (hereinafter “ERU”) were constructed with the purpose of measuring on-reef oyster recruitment and survival at the three study sites. Mixed concrete substrate used for artificial reef construction at several sites in Louisiana was cut into blocks approximately 21 cm × 16 cm × 10 cm (length × width × height) and attached to the end of 60 cm long polyvinyl chloride poles using marine epoxy. These poles were pushed into the bottom sediment, so the blocks were 8–10 cm off the bottom. Nine (9) ERUs were deployed at each study site in April 2011 and were removed for analysis in October 2012. Experimental reef units were placed approximately 10 m from the ALS bags. All attached oysters and spat (both live and dead) were counted and their shell heights measured (millimeters). Size class of recruited oysters was binned in 10 mm increments for analysis. Counts of oysters on each block were converted to density estimates, using the calculated surface area of each ERU (number of oysters per square meter).

#### Statistical Analyses

Salinity and temperature data were analyzed by site using a one-factor analysis of variance (ANOVA) for 2011 and 2012 separately. For 2011, interval salinity, interval growth rates, *Perkinsus marinus* infection intensity, and condition index were examined using a repeated measures ANOVA with an autoregressive correlation structure and a random statement to account for temporal correlation in the data (Proc Mixed, SAS 9.3; Fixed factor: site; random: interval; subject = bag) followed by LSMeans post hoc ( $\alpha < 0.05$ ) when significant differences were found. The random rather than the repeated statement was used because the G matrix was parameterized. Cumulative mortality (%) at the end of the study at the last sampling (October 2011) was analyzed using Proc Mixed (fixed factor: site; random: bag) and a Tukey’s test when significant differences were found.

For 2012, interval salinity, interval growth rates, *Perkinsus marinus* infection intensity, and condition index were analyzed by site using a repeated measures ANOVA within auto re-

gressive correlation structure and a random statement to account for temporal correlation in the data (Proc Mixed, SAS 9.3, Fixed factors: stock, site; random: interval, subject: oyster) followed by LSMeans post hoc comparison ( $\alpha < 0.05$ ) when significances were found. Cumulative mortality (%) in June and November 2012 were analyzed by site using Proc Mixed (factor: stock, random: bag) and Tukey’s test when significant differences were found. Experimental reef unit oyster density and size data were analyzed by site using Proc Mixed (fixed factor: site; random: block) followed by a Tukey’s test when significance differences were found.

## RESULTS

#### Water Quality

Mean annual water temperature for 2011 and 2012 ranged from 22.5 to 25.5°C and was similar at all three sites within both years ( $P = 0.2$ ) (Table 1; Fig. 2). Mean salinity differed significantly by site ( $P < 0.0001$ ). Throughout the 2 y, VB had lowest mean salinity, whereas GI had highest mean salinity. Temperature did not differ significantly between sites in 2011. In 2012, GI was significantly warmer than the other two sites, but the difference in mean temperature was less than 1°C.

#### Off-Reef Growth, Mortality, Condition, and Parasitic Infection—2011

Interval growth rate ( $\text{mm mo}^{-1}$ ) of BS stock oysters was significantly affected by the interaction of the site and interval ( $F_{6,9} = 7.13$ ;  $P < 0.01$ ; Fig. 3). Oysters deployed in GI had highest growth rates overall in Feb–Apr time frame ( $>6 \text{ mm mo}^{-1}$ ), whereas oysters at VB had significantly lower growth rates in Jun–Aug interval ( $<0.5 \text{ mm mo}^{-1}$ ). All other sites by interval combinations had similar growth rates, ranging in means from 1.0 to  $3.4 \text{ mm mo}^{-1}$ .

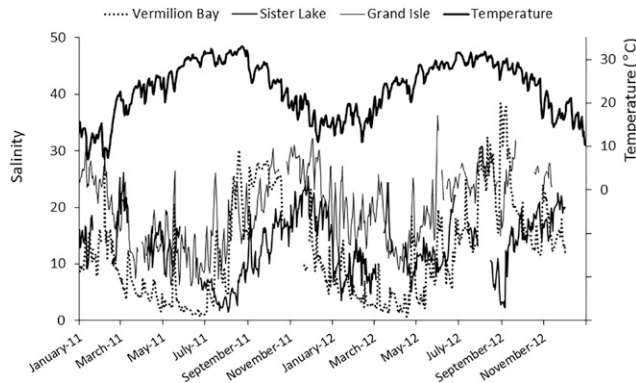
Cumulative mortality of BS stock oysters differed significantly by site (Fig. 3). Oysters deployed in VB in 2011 had significantly higher cumulative mortality (89%) as compared with oysters deployed in GI in 2011 (30%), and both oyster groups had significantly greater cumulative mortalities than oyster deployed in SL ( $<11\%$ ).

Condition index was significantly affected by the interaction of interval and site ( $F_{2,55} = 25.3$ ;  $P < 0.01$ ). Grand Isle had the highest condition index, although it declined from February through October. Sister Lake oyster condition declined from February to June, but condition remained consistent through October. Vermilion Bay did not have enough oysters alive in October to calculate condition index. *Perkinsus marinus* infection intensity was low throughout the year at all sites (mean

TABLE 1.

Minimum, maximum, mean, and standard error (SE) salinity and temperature for 2011 and 2012 at the three study sites.

	2011				2012			
	Salinity		Temperature (°C)		Salinity		Temperature (°C)	
	Min–Max	Mean (SE)	Min–Max	Mean (SE)	Min–Max	Mean (SE)	Min–Max	Mean (SE)
Vermilion Bay	0.7–30.1	8.6 (0.4)	4.8–33.6	22.5 (0.5)	0.6–38.5	12.6 (0.5)	8.8–32.5	23.9 (0.3)
Sister Lake	1.5–26.1	13.3 (0.3)	5.9–32.3	22.9 (0.4)	2.2–24.4	12.7 (0.3)	10.5–32.0	24.2 (0.3)
Grand Isle	6.1–32.2	19.2 (0.3)	9.1–33.3	22.8 (0.3)	8.9–36.3	21.1 (0.4)	13.4–32.2	25.5 (0.3)



**Figure 2.** Daily salinity for Vermilion Bay, Sister Lake, and Grand Isle from January 2011 through December 2012. The gray solid line indicates mean temperature ( $^{\circ}\text{C}$ ) for the three sites, which did not differ when data were available for all three sites. Data originate from United States Geological Survey (USGS) recorders within Sister Lake (USGS7381349) and Grand Isle (USGS73802516) and Coastwide Reference Monitoring Station (CRMS) in Vermilion Bay (CRMS0541).

$\pm$  SE:  $8,600 \pm 3,800$ ; range: 0–200,000 parasites  $\text{g}^{-1}$  oyster tissue).

#### Off-Reef Growth, Mortality, Condition, and Parasitic Infection—2012

Breton Sound and SL stock oysters located in GI were removed from the growth rate analysis after June because of the burial of the cages after Hurricane Isaac in August; in VB, BS stock was removed after February because of burial. All sites had a significant stock  $\times$  interval interaction (SL:  $F_{8,248} = 2.18$ ;  $P < 0.03$ ; VB:  $F_{8,278} = 2.10$ ,  $P < 0.04$ ; GI:  $F_{6,257} = 2.62$ ;  $P = 0.018$ ; Fig. 4).

Sister Lake had significantly reduced the growth of LC stock in Feb–Apr, and all stocks had significantly lowest growth

(<0.5  $\text{mm mo}^{-1}$ ) from April to August. The remaining intervals (Dec–Feb, Feb–Apr, and Aug–Oct) had significantly higher growth rates for all stocks (>2.5  $\text{mm mo}^{-1}$ ), except LC stock in Feb–Apr ( $1.3 \pm 0.2 \text{ mm mo}^{-1}$ ).

In contrast, all stocks at VB had extremely low growth rates in Dec through Apr, while interval salinity remained below seven, and temperatures remained low (<25 $^{\circ}\text{C}$ ). Significantly higher growth rates of all stocks were recorded for the remaining interval periods (>2.5  $\text{mm mo}^{-1}$ ) with higher temperatures and salinities (except Apr–Jun where salinity remained low but temperature increased), except for LC stock in Jun–Aug which had low growth (<0.2  $\text{mm mo}^{-1}$ ).

All stocks in GI had similar growth rates through all periods except for Jun–Aug when highest temperatures were recorded despite interval salinities remaining above 15 through all periods.

In June 2012, cumulative mortality was significantly affected by the site and stock interaction ( $F_{8,412} = 7.71$ ,  $P < 0.0001$ ) with all three stocks in GI having significantly higher cumulative mortality as compared with all other stock and site combinations which had less than 8% cumulative mortality by June (Fig. 5). In October, cumulative mortality was significantly affected by the site and stock interaction ( $F_{8,250} = 8.31$ ;  $P < 0.0001$ ). Lake Calcasieu stock oysters in GI had significantly higher cumulative mortality (20%) as compared with all other stock by site combinations. All other stock by site combinations had cumulative mortalities less than 15%.

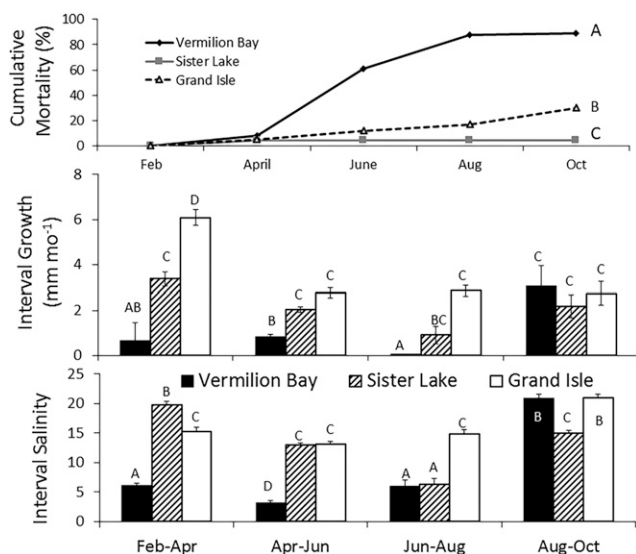
Owing to a limited number of available seed oysters, LC stock was not included in the analyses of parasite infection or condition index in 2012. Condition index was significantly affected by interval for all three sites (Fig. 6) with a trend of decreasing condition from December through August (GI:  $F_{2, 32.2} = 154.04$ ,  $P < 0.0001$ ; SL:  $F_{2, 34.5} = 100.10$ ,  $P < 0.0001$ ; Vermilion:  $F_{2, 34.9} = 157.02$ ,  $P < 0.0001$ ). Overall infection intensity in 2012 was light [mean (SE): 2,607.4 (1,114.5) parasites/g wet tissue], and only GI had a significant difference, by interval with April being lower than August samples, which had the highest temperatures ( $F_{2, 80} = 4.26$ ,  $P < 0.0175$ ).

#### Experimental Reef Unit Population Demography and Density

All nine ERUs deployed in March 2011 were recovered from VB in October 2012; seven were recovered from both SL and GI. Evidence of spat settlement was noted on all 23 recovered ERUs. Density of live and dead oysters (scars) was significantly higher at GI ( $F_{2,20} = 48.36$ ,  $P < 0.0001$ ; mean  $\pm$  SE:  $74.2 \pm 9.2 \text{ ind m}^{-2}$ ;  $P < 0.0001$ ) as compared with SL ( $5.5 \pm 1.3 \text{ ind m}^{-2}$ ) and VB ( $18.3 \pm 2.1 \text{ ind m}^{-2}$ ; Fig. 7). Whereas SL and Vermilion had 100% live oysters, all GI oysters were dead in October 2012. Mean oyster size differed significantly between the three sites ( $F_{3, 112} = 1307.09$ ,  $P < 0.0001$ ) (Fig. 7). Vermilion Bay ERU supported the largest oysters, with a mean size of live oysters of  $85.6 \pm 2.2 \text{ mm}$ . Sister Lake live oysters had a mean size of  $62.7 \pm 3.8 \text{ mm}$ . There were no live oysters on GI ERU, but measured spat scars averaged  $39.3 \pm 1.8 \text{ mm}$  in size, indicative of mortality early on.

#### DISCUSSION

Restoration of oyster reefs requires understanding how dominant environmental conditions influence both oyster pop-



**Figure 3.** Cumulative mortality (%; top), mean (SE) interval growth ( $\text{mm mo}^{-1}$ ; middle), and salinity (bottom) of Breton Sound stock oysters (BS) deployed in February 2011 in Vermilion Bay (VB), Sister Lake (SL), and Grand Isle (GI). Different letters represent statistically significant differences ( $P < 0.05$ ).

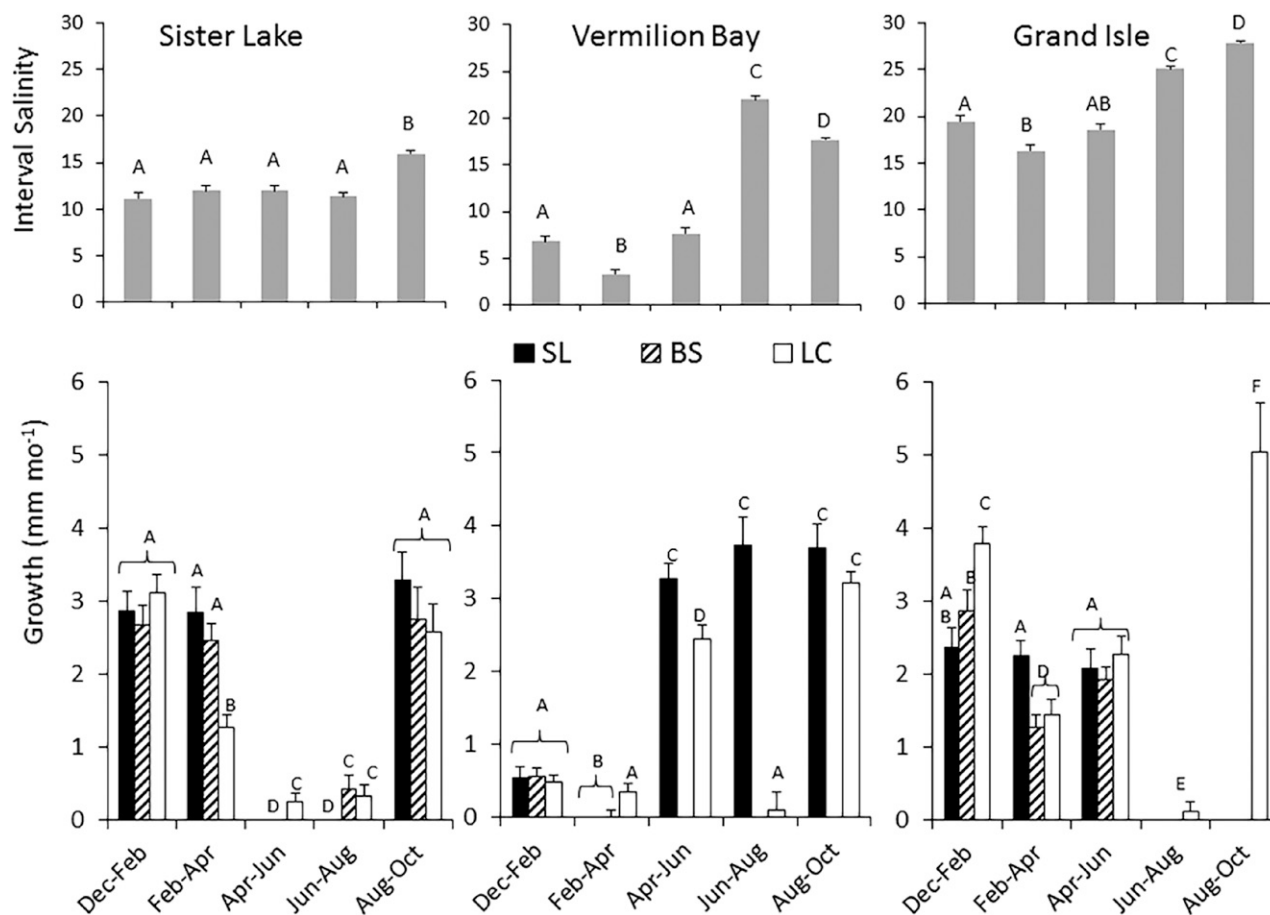


Figure 4. Interval salinity (mean ± SE) and interval growth (mm mo<sup>-1</sup>; mean ± SE) of three oyster stocks (Sister Lake, SL; Breton Sound, BS; and Lake Calcasieu, LC) deployed in three locations (Sister Lake, Vermilion Bay, and Grand Isle) from December 2011 through November 2012. Hurricane Isaac, which passed over the Grand Isle site in August 2012, resulted in loss of the Sister Lake and Breton Sound oysters bags in August 2012. Breton Sound oysters were buried at Vermilion Bay and not included after April 2012. Some missing data from data recorders may result in over or underestimation of interval salinities (Fig. 2) in some instances. Different letters represent statistically significant differences ( $P < 0.05$ ).

ulation attributes (recruitment, growth, and mortality) and biotic and abiotic interactions (predation and disease) (Coen & Luckenbach 2000, Brumbaugh & Coen 2009, Beseres Pollack et al. 2012, Baggett et al. 2015). Over a 2-y period, the highest salinity sites demonstrated low likelihood for development of a sustainable reef over time because of on-reef mortality, whereas the midsalinity site with low mortality and moderate natural recruitment represented the most likely site for development of a sustainable reef. In contrast, the low-salinity site experienced extreme variability in salinity between the 2 y, suggesting that timing of restoration would be extremely important. Low levels of on-reef recruitment at the low and midsalinity sites suggest that seeding of these reefs could be beneficial if appropriate stocks are identified. In this study, despite lower environmental condition differences than expected, there were indications of differences in stock performance (growth) at sites, indicating that selection of appropriate stocks and seeding of low recruitment reefs could prove useful for restoration.

Numerous studies support the findings that much of the observed variation in oyster population dynamics can be explained by both the direct and indirect effects of temperature and salinity, alone, and their interaction (e.g., Gregalis et al.

2009, Stricklin et al. 2009, Beseres Pollack et al. 2012). Oysters can endure low salinity for short periods of time; however, frequent or extended low salinities especially at elevated temperatures can be detrimental to the entire oyster population (Butler 1952, Loosanoff 1953, La Peyre et al. 2003, 2009, 2013c, Munroe et al. 2013, Rybovich et al. 2016). The low-salinity site (VB) experienced salinities below 5 for much of 2011 and the first half of 2012 (Fig. 2). In 2011, this resulted in high mortality of caged oysters, whereas in 2012, oysters survived and grew; however, timing of restoration projects could be critical as recruitment and growth to larger size classes which may withstand extended salinities would be critical. Whereas extended low salinities (i.e., <2 for 2 mo) are considered lethal to oyster populations, extended salinities below 10, such as the mean salinity at VB in 2011, can also impact oyster population development. For example, low salinities may reduce filtration by the oyster thus decreasing food intake and potential growth (Loosanoff 1953, Hofmann & Powell 1998). A correlation between low spring/summer salinity and reduced larval recruitment and growth has also been observed (Loosanoff 1953, Butler 1954, Hofstetter 1983, Ortega & Sutherland 1992). Frequency, duration, and timing of low-salinity events from long-term salinity records can be important in predicting

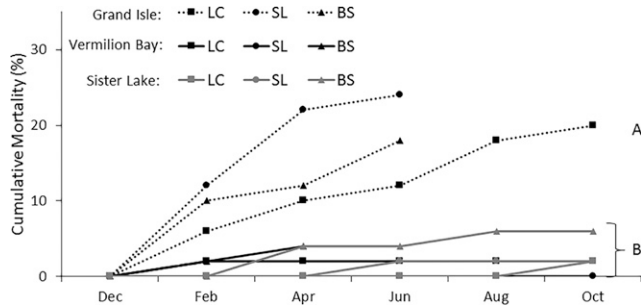


Figure 5. Cumulative mortality of three oyster stocks (Sister Lake, SL; Breton Sound, BS; and Lake Calcasieu, LC) deployed in three locations (Sister Lake, SL; Vermilion Bay, VB; and Grand Isle, GI) from December 2011 through November 2012. Different letters represent statistically significant differences ( $P < 0.05$ ).

reef development and sustainability (i.e., Soniat & Brody 1988, Beseres Pollack et al. 2012).

High salinity may also have significant negative impacts on oyster population success through effects on predators and disease. High salinity alone increases the risk of predation (Wells 1961, Shumway 1996, White & Wilson 1996), and high salinity during high temperatures favors *Perkinsus marinus* infection (Ogle & Flurry 1980, Craig et al. 1989, Ragone Calvo et al. 2003). Along the Gulf coast, predation on subtidal oyster reefs often overwhelms recruitment and growth when mean salinities exceed 15 (Menzel et al. 1966, Garton & Stickle 1980, Brown & Haight 1992). For example, southern oyster drills (*Stramonita haemastoma*) are very effective predators, especially at salinities above 15 (Garton & Stickle 1980), and have shown preference for smaller oysters including spat (Brown

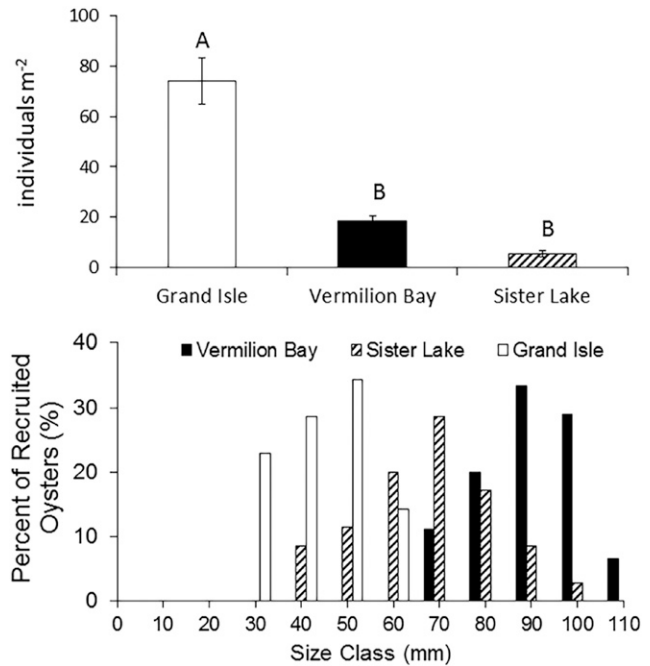


Figure 7. Recruitment density (# individuals per square meter, mean  $\pm$  SE, TOP) and percent of oysters by size class (mm) of both live and dead recruited individuals on the experimental reef units (ERUs) deployed for 18 mo in Grand Isle, Vermilion Bay, and Sister Lake. One hundred percent (100%) of recruitment on Grand Isle ERU were dead; >80% of Vermilion Bay and Sister Lake recruitment were live. Different letters represent statistically significant differences ( $P < 0.05$ ).

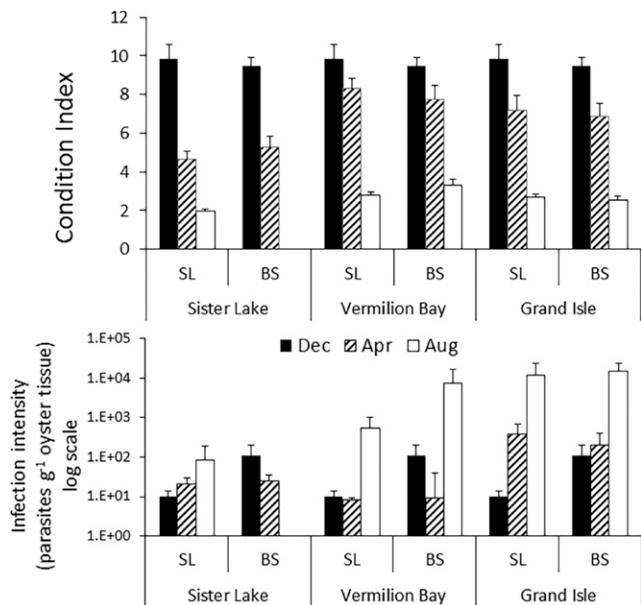


Figure 6. Condition index (top) and log of *Perkinsus marinus* infection intensity (bottom, mean  $\pm$  SE) of three oyster stocks (Sister Lake, SL; Breton Sound, BS; and Lake Calcasieu, LC) deployed in three locations (Sister Lake, SL; Vermilion Bay, VB; and Grand Isle, GI) from December 2011 through November 2012. Different letters represent statistically significant differences ( $P < 0.05$ ).

1997). Other invertebrate predators, including the Gulf of Mexico stone crab (*Menippe adina*) (Brown & Haight 1992), Florida stone crab (*Menippe mercenaria*) (Menzel et al. 1966), and the blue crab (*Callinectes sapidus*) (Eggleston 1990) also prey on smaller oysters.

High predation pressure at the highest salinity site (GI) appears to negate opportunities for restoration *in situ*. The GI area is known to have high populations of *Stramonita haemastoma*, and experimental cages and reefs were covered with a high density of these drills. Whereas the Louisiana Sea Grant Oyster Hatchery is located on GI as the area supports high oyster growth within aquaculture systems, on-reef (uncaged) oysters failed to survive to adult size. Furthermore, the low to moderate infection intensities (<200,000 parasites per gram wet tissue) in caged oysters at the high-salinity site during this study fail to explain the observed mortalities on the experimental reefs (Fig. 6). In addition, the 30% mortality of oysters in cages in GI is not explained by salinity, temperature, or disease and, in fact, offers further evidence of potential predation limitation as only single-walled cages were used and drills noted on several occasions in the cage. The experimental reef data are from bioengineered concrete blocks which, lacking high interstitial space, may have limited refuge initially. Reef design may contribute to early development of an oyster reef by influencing predation refuge of substrate provided (Soniat et al. 2004, Dunn et al. 2014, George et al. 2015). At the same time, monitoring of adjacent reefs constructed with vertical shell bags also found a lack of live oysters or scars greater than 60 mm (La Peyre et al. 2013b) suggesting that increasing refuge may not help at this site.



Whereas the overall site mean salinity may be important in determining site suitability, estuarine sites tend to have enormous variation (ranges of mean daily salinity at all three sites exceeded 24; Table 1), and the timing of low or high salinity with temperature can be critical for determining oyster population development (Butler 1952, Dugas & Roussel 1983, La Peyre et al. 2003, La Peyre et al. 2013c). In the spring of 2011, major rainstorms combined with regular spring snowmelt caused massive flooding of the Mississippi River basin. To reduce the impact on major urban and residential areas, flood control structures were opened to divert excess floodwaters from the Mississippi River allowing huge volumes of fresh water to enter the surrounding marsh. Vermilion Bay, SL, and GI all experienced a significant decrease in salinity from April to June 2011 (Fig. 2); however, the impact may have been most dramatic in VB, where mean salinity dipped below two, and oysters experienced more than 60% mortality during this period (Fig. 3). By contrast, this spring/early summer drop in salinity was likely beneficial to the other sites as low spring-time salinities have been shown to reduce disease intensity (La Peyre et al. 2003) and prevented high infection intensities development at SL and GI sites. With increasing management and control of river flows, management that controls freshwater flow into estuaries which are timed to minimize negative impacts to oyster growth and maximize benefits may be useful (La Peyre et al. 2009).

High interannual variation in recruitment, growth, and mortality complicate identification of sites for restoration based on short-term assessments. For example, whereas the low-salinity site, Vermilion Bay, experienced good recruitment, growth, and survival in 2012, analysis of long-term salinity data suggests that 2012 was an unusually high-salinity year; mean long-term and spawning period salinities generally average less than 5, with almost regular annual periods of extended low salinity (<2; >30 days). Long-term (>10 y) data sets are suggested as a requirement for understanding oyster reef development and maintenance (Mann et al. 2009, Powell et al. 2009, Harding et al. 2010, 2012, Soniat et al. 2012). These long-term data are critical because of high interannual fluctuations in natural recruitment (i.e., Galtsoff et al. 1947, Southworth & Mann 2004, Powell et al. 2008) combined with detectable impacts of long-term weather patterns on oyster reef populations (i.e., ENSO, Soniat et al. 2012, Powell 2017). As oyster population sustainability and reef maintenance (accretion) are dependent on the balance between recruitment, mortality, and shell life, factors which affect any component of the oyster population and shell accretion processes need to be considered in combination and over appropriate time periods.

Recent studies suggest genetic differentiation of oyster stocks, with some explicitly examining gene expression and stock performance in relation to salinity (i.e., Eierman & Hare 2016, Leonhardt et al. 2017). For example, Leonhardt et al. (2017) found that stocks were genetically differentiated with respect to low-salinity tolerance (SL stock) and dermo-related mortality (LC stock). Similar to Leonhardt et al. (2017) who examined stock performance across a salinity gradient in one Louisiana estuary, this study examined stock performance across sites which had been selected to reflect differences in salinities. Although some of the same oyster stocks were examined, the results were not as clear cut (Figs. 4 and 5). This may be because the study failed to experience the same range of

conditions in salinity, particularly with the low-salinity site experiencing an unusually high-salinity year in 2012. Furthermore, by using sites within different estuarine basins, the variability and timing in variability of salinity changes also differed making comparisons difficult.

Further examination or testing of stocks bred for specific conditions may be useful, particularly as discussions about seeding reefs, in areas which might be recruitment limited, or with changing rapid environmental conditions exist. Powell (2017) suggests a long-term declining trend of reproductive capacity in GoM oysters related to warming water temperatures and disease interactions. If this trend continues, seeding of reefs may be necessary. Seeding of reefs may also be useful to reduce predation risk as predation and oyster size have been to be negatively correlated (Newell et al. 2000, Kulp et al. 2011) or possibly when environmental conditions are changing rapidly suggesting stock other than local populations might be beneficial. In areas not recruitment limited, seeding may not be beneficial as high natural recruitment can easily overwhelm seeding efforts (Geraldi et al. 2013).

Despite the continued investment of resources, money, and time, oyster reef restoration has had varied success (Mann & Powell 2007, La Peyre et al. 2014). In many cases, reef failure can be attributed to poor site selection, specifically from installing substrate in a location that does not support self-sustaining recruitment, growth, and survival of oysters (e.g., Scyphers et al. 2011; La Peyre et al. 2017). Natural recruitment on available substrate and survival of these individuals to large oysters (>60 mm) remain one of the more difficult aspects of reef development to predict but may be the most vital to long-term reef success (i.e., Powell & Klinck 2007, Bumbaugh & Coen 2009, Puckett & Eggleston 2012, Theuerkauf et al. 2015, Casas et al. 2015, George et al. 2015). Integrating field observation and *in situ* data collection with modeling efforts and GIS-based methods may significantly improve oyster reef restoration success (Johnson et al. 2009). Data from this work, for example, help better define conditions for *in situ* natural recruitment and survival to large oysters (>60 mm). Historical population models and habitat suitability indices have been developed to better inform management decisions; however, these do not consistently include on-reef recruitment, the effects of predation, parasitic infection, or some combination thereof. Models that account for complex interactions will help increase the likelihood of restoration effectiveness (Johnson et al. 2009).

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